RESEARCH ARTICLE

Assessing the invasion potential of five common exotic vine species in temperate Australian rainforests

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Abstract

To compare the capacity of native and exotic vine species established under a rainforest canopy, a comparison of growth rates and resource allocation was made amongst five exotic vine species that are serious and common invaders and two common native vine species under two light conditions reflective of edge and interior canopy conditions. All species experienced heavy reductions in growth parameters in the low-light treatment, but three exotic species showed stronger growth under the low light. All exotic species had higher plasticity in leaf morphology showing a significant increase in SLA under low light. Native vines may have a lower capacity to change leaf morphology in shade, as a result of local adaptation to edge habitats. Higher SLA under both low and high light conditions suggests that exotic vines species are able to exploit a range of forest conditions better than the native species. Three species, *Anredera cordifolia*, *Araujia sericifera* and *Cardiospermum grandiflorum*, appear particularly capable of invading rainforest interiors. Individuals produced few leaves, focusing resources on roots and stems suggesting a response to reach the canopy quickly. With their long-distance seed dispersal, plasticity in leaf SLA and high RGR, these species appear most likely to invade undisturbed rainforest.

Keywords

Introduction

In forests, vines can cause structural damage to the canopy, reduce light availability and increase competition for underground resources, which results in reduced growth and survival of host and neighbouring trees (Estrada-Villegas and Schnitzer 2018). This fast growth strategy is achievable as vines do not invest biomass into self-supporting structures and therefore, they invest more in growth and reproductive structures. Compared to other woody plants, vines tend to be situated on the "faster end" of the life-history spectrum (Westoby et al. 2004), through having higher specific leaf area (SLA) (Llorens and Leishman 2008; Mello et al. 2020), higher photosynthetic capacity (Mello et al. 2020) and more investment into stem growth (Ichihashi and Tateno 2015). The difference in traits between vines and trees, as well as the negative impacts of vines on trees is well studied, especially in tropical systems (Ingwell et al. 2010; Estrada-Villegas and Schnitzer 2018; Mello et al. 2020); however, there is also overlap in trait values between some vines and trees, as well as amongst species of invasive and native vine species (Llorens and Leishman 2008; Osunkoya et al. 2010, 2014; French et al. 2017; Mello et al. 2020).

In a meta-analysis of 117 studies, Van Kleunen et al. (2010) compared traits across studies comparing invasive and native plants species that co-occurred, many co-familial. Invasive plant species had higher SLA, higher photosynthetic capability and faster growth rates than native species (Van Kleunen et al. 2010). There is some evidence that the pattern is also true when vines are considered separately. Greenhouse studies in tropical areas (Osunkoya et al. 2010, 2014) showed that four common invasive vine species in eastern Australia have higher photosynthetic capability, SLA and phenotypic plasticity than for common functionally similar native species, although relative growth rates were not different. This suggests that invasiveness is associated with a set of traits that provide a competitive advantage. However, there are other factors that influence invasiveness, such as release from herbivores (Keane and Crawley 2002) and whether the invasive environment is adequate to successfully reproduce and disperse (Van Kleunen et al. 2015). We predict that, if native vines show similar growth and plasticity to invading exotic invasive vines, then other factors, such as release from herbivores and pathogens may be particularly important to allow them to invade and become abundant. Furthermore, if a particular set of traits are critical in invasiveness, then we would predict that native species which can dominate sites and be extremely abundant would show similar invasive traits. A study in a temperate, moist sclerophyll forest found little difference in above-ground biomass allocation between invasive and native vine species (Llorens and Leishman 2008), which could indicate that other factors give exotic invasive vines a competitive advantage. Furthermore, there was no difference found in the height reached or percentage of host height reached between exotic invasive species and native species, suggesting that there was little difference in impact on the community between exotic invasive and native vine species.

Increased investment in growth can be allocated to roots, stems or leaves. Higher investment into stem elongation can be particularly beneficial as it allows the vine

to reach higher into the canopy quickly and, thus, gain more light for photosynthesis (Falster and Westoby 2003; Llorens and Leishman 2008). However, investment into stem elongation must be balanced adequately with the other needs of the vine to survive and reproduce. If exotic invasive vines are released from herbivores, then stem elongation to get their leaves into the light would be the most beneficial strategy. Therefore, we predict that exotic invasive vine species are likely to invest more into stem growth than leaf growth compared to native vine species.

While vine invasion is particularly problematic at the light-filled edges of rainforest patches, the ability to grow and establish in the forest interior would be an invasive characteristic that increases the risk and impacts of that species in closed forests. The plasticity to change growth parameters in low-light situations is, thus, an important part of identifying exotic invasive species that pose the greatest risk. Some invasive vine species are considered more problematic in forests than others due to apparent high growth rates or high propagule pressure. In Australia, there are at least 179 species of exotic vines (Harris et al. 2007), though not all are considered equal threats to biodiversity. It is likely that the species that should be considered to be greater threats should have higher photosynthetic ability, invest more into stem elongation and, consequently, have higher growth rates as well as show high rates of growth even in interior light conditions. Furthermore, knowledge of how invasive and native vine species differ in these traits with light availability can help to predict the species that can exploit disturbances better or can invade undisturbed interiors. At present, information on growth rates and resource allocation under differing light levels is poorly understood for all exotic vine species in Australia, preventing good risk assessments and prioritisation in management. Collectively, invasion and establishment of exotic vines and scramblers are listed as a key threatening process in New South Wales (NSW) where 38 entities are listed as affected by vines and scramblers. However the list of vines and scramblers includes species that are much less abundant and problematic and some that occur frequently (A. Bernich and K. French, unpublished data).

In order to help evaluate the invasiveness of key exotic invasive vine species, we assessed growth rates of five common invasive exotic vine species in eastern Australia and two common native species on host trees in a shade house with two shade treatments. We measured relative growth rates (RGR), stem lengths, proportion of biomass allocated to leaves, stems and roots and specific leaf area. We predicted that individuals of each species grown in less shade will have higher RGR and longer stem lengths, though lower SLA. We predicted that invasive species will also have higher RGR and stem lengths and higher SLA indicating higher photosynthetic efficiency, which then leads to relatively less investment in leaves and more relative investment into stems and roots compared to native species. We also predicted that differences in trait values would occur amongst species and show that some species are able to exploit establishment opportunities under the rainforest canopy. One of the native species, *Cissus antarctica*, is especially abundant at the edge of disturbed rainforests in eastern Australia where it can dominate and smother canopy causing significant harm to native host species. There is concern that such dominance may cause forest interiors to become degraded.

Methods

Study species

We grew seven vine species, five exotic invasive species (*Anredera cordifolia*, *Araujia sericifera*, *Cardiospermum grandiflorum*, *Delairea odorata* and *Ipomoea cairica*) and two native species (*Cissus antarctica* and *Pandorea pandorana*). All species are commonly found in rainforests, wet sclerophyll forests and disturbed sites on the east coast of Australia. *Anredera cordifolia* (family Basellaceae) is a semi-succulent twiner from South America, that is listed as a Weed of National Significance in Australia. It was introduced in the early 1900s (Vivian-Smith et al. 2007) and quickly establishes at sites through vegetative reproduction via aerial tubers. *Araujia sericifera* (family Apocynaceae) is a South American twiner also introduced in the early 1900s, which disperses by producing masses of windblown seeds. *Cardiospermum grandiflorum* (family Sapindaceae) is a tendril climber from South America, introduced in the 1920s, with multiple seeds in a papery "balloon" that can be distributed by wind and water. *Delairea odorata* (family Asteraceae) is an herbaceous twiner or scrambler from Africa that was introduced in the early 1900s, that spreads locally through vegetative reproduction (stolons and stem fragments), although it also produces viable seeds in Australia. *Ipomoea cairica* (family Convolvulaceae) is a twiner from tropical Africa and Asia and was introduced in the 1840s, it is common in coastal eastern Australia and can withstand a wide range of environmental conditions (Liu et al. 2016a). The native *Cissus antarctica* (family Vitaceae) is a tendril climber that can grow thick stems (up to 15 cm in diameter) and is abundant along the east coast of Australia, producing a fleshy fruit. *Pandorea pandorana* (family Bignoniaceae) is a large woody twiner that is also abundant in eastern Australia, producing winged seeds.

Vine species were all collected from forests near Wollongong, with some species being grown as ~ 30 cm cuttings (*D. odorata*, *I. cairica*, *P. pandorana* and *C. antarctica*), from seeds (*C. grandiflorum*), tubers (*A. cordifolia*) or harvested seedlings (*A. sericifera*) which had the first two true leaves, around 5–15 cm in height. We attempted to grow both *C. grandiflorum* and *A. sericifera* as cuttings, though no *C. grandiflorum* cuttings were successful and there was only a 10% success rate for *A. sericifera*. Propagules for all species were collected in September 2021 and were grown until sufficient individuals were established to be used in the experiment. All propagules were collected along forest edges (i.e. tracks or clearings) which were more representative of the medium light treatment (see below). As establishment times varied amongst species, the date that species were potted and placed next to a host tree occurred over two months at the beginning of the Austral Summer (late October – mid December).

All vine individuals were grown on *Acmena smithii* (cultivar 'Speedy Screener', family Myrtaceae) host trees that were potted in 300 mm pots. The host trees ranged in height from 1 m to 1.8 m tall. *Acmena smithii* is a common tree in eastern Australia that grows in rainforests and wet sclerophyll forests.

Experimental design

All vines and host trees were grown in a shade house at the University of Wollongong, NSW 34.4054°S, 150.8784°E. The shade house had two sections, one with low light penetration to mimic the understorey under a rainforest canopy and one with medium light to mimic a gap in a rainforest or rainforest edge. The roof of the low light section was covered in two layers of shade cloth, which allowed 2% of light to reach the floor (similar to 85–95% canopy cover), whereas the medium light section had one layer of medium shade cloth, which allowed 30% of light to reach the floor (similar to 50–60% canopy cover).

Six individuals of each species were randomly selected for the medium light and low light treatments and were transplanted into 300 mm pots filled with commercial potting mix (Osmocote Premium) and given 25 g of slow-release fertiliser (Power-Feed 500 g All Purpose Controlled Release). They were then placed adjacent (on the southern side) to an *A. smithii* individual in their allocated shaded areas. Two to four extra individuals were harvested and dried in an oven at 65 °C for five days to measure dry biomass of roots, stems and leaves at the start of the experiment (the difference in number of individuals for each species was due to the death of some individuals before they could be dried out). Vines and trees were watered by an automatic dripper system attached to a tap timer, with each plant having a dripper spike in the soil of the pot. Plants were drip-watered for 10 minutes at 6 am and 6 pm every day.

The experiment for each species began when plants were placed next to the host plant. Initial plant sizes are shown in Suppl. material 3. Vines were grown for 24 weeks, after which time, vines were removed from host trees and laid horizontally on the ground to measure the longest stem (from the junction of the roots and the stem to the tip of the longest stem, to give a measurement of the potential height each individual could reach). Ten leaves for each vine individual were removed and measured using a Li-Cor leaf area meter (Model Li-3000A, Lincoln, Nebraska, USA), then put into separate labelled bags for drying (65 °C for 5 days), before being weighed and specific leaf area calculated (SLA = leaf area/dry weight). Then, each individual was sorted into leaves, stems, aerial tubers (for *A. cordifolia*) and roots, with roots being washed to remove soil, before being placed in a drying oven at 65 °C for 5 days and then weighed. Relative growth rate (RGR) was calculated using the formula:

$$RGR = \frac{lnDW_f - lnDW_i}{no.\,of\,days}$$

where DW_f is the total dry weight at the end of the experiment for an individual and DW_i is the average dry weights of the plants sacrificed at the beginning of the experiment for the species being tested.

The dry weights of each plant part (roots, stems and leaves) were divided by the total dry weight to give percentages of biomass allocation; these parameters are referred

to as root mass fraction (RMF), stem mass fraction (SMF) and leaf mass fraction (LMF). For *A. cordifolia*, aerial tuber weight was added to RMF as a measure of investment into energy storage; however, the proportion of biomass invested into aerial tubers by *A. cordifolia* was also recorded separately. Traits were only measured on individuals that did not die in the experimental period.

Data analysis

We used a Bayesian modelling approach to estimate the distribution of values for each of the measured plant variables for each combination of species and shade treatment. The fitted distributions were then used to estimate the magnitude and direction of differences in response between species within each treatment and between treatments for each species. Stem height and SLA values, which could only be positive, were modelled as gamma-distributed variables with the shape parameter of the distribution being allowed to vary between shade treatments. RGR values were modelled as being drawn from a Student-t distribution since values could be negative and some outliers were evident in the observed data. The shape (degrees of freedom) parameter of the distribution was treated as an unknown quantity to be estimated by the model, while the scale parameter (standard deviation) was allowed to vary between treatments. The proportion of biomass allocated to each of leaf, stem and root fractions was modelled using Dirichlet regression.

Models were fitted by Hamiltonian Monte Carlo sampling via the "brms" package version 2.18 (Bürkner 2017) in R version 4.2.1 (R Core Team 2022). For all models, we set weakly informative prior distributions for parameters, as recommended by Gelman (2009) and van de Schoot (2021), to ensure that fitted distributions reflected the observed data while constraining the model fitting process from exploring unrealistic ranges of parameter values. For the Dirichlet regression of biomass allocation fractions, we explored alternative choices for prior distributions on the intercept and regression coefficients using prior predictive simulation. This involved fitting the model, based only on candidate prior distributions, i.e. with no observed data. The simulations highlighted the potential sensitivity of model predictions to the choice of standard deviation for the Normal priors on the intercept and regression coefficients. Given this, we chose to treat the prior standard deviation as an additional parameter to be learned from the data and set an exponential hyper-prior distribution on it.

For each model, we ran four Markov chains with 5000 iterations and 1000 warmup iterations. Model convergence was assessed using the Gelman-Rubin statistic, which showed convergence for all models and by checking for an adequate number of effectively independent samples to ensure reliable estimates of the tails of the fitted distributions. In addition, we graphed posterior model predictions together with observed data values for each measured variable to check for any disagreement that might indicate a problem with model structure or convergence.

For all models other than stem growth rate, the distribution of differences in response between each pair of species within each shade treatment was estimated by subtracting posterior predictions of mean response for one species from those for the

other species. For the stem growth rate model, difference calculations were based on posterior predictions of median rather than mean response as some observed values were close to zero, which resulted in a strongly right-tailed posterior distribution for which the median is a more representative summary statistic.

Results

At the end of the six months, two *A. sericifera* individuals had died in the medium light treatment. In the low light treatment 10 deaths occurred: three *I. cairica* individuals, two *D. odorata*, three *A. sericifera*, one *C. antarctica* and one *P. pandorana*.

Relative growth rate

For all species, mean RGR was consistently higher when grown under medium light compared to low light, with no overlap in the 95% range of predicted mean RGR values (Fig. 1, Table 1). Two exotic vines did poorly in low light, *D. odorata* (93% reduction in mean predicted RGR) and *I. cairica* (75% reduction) and the two native spe-
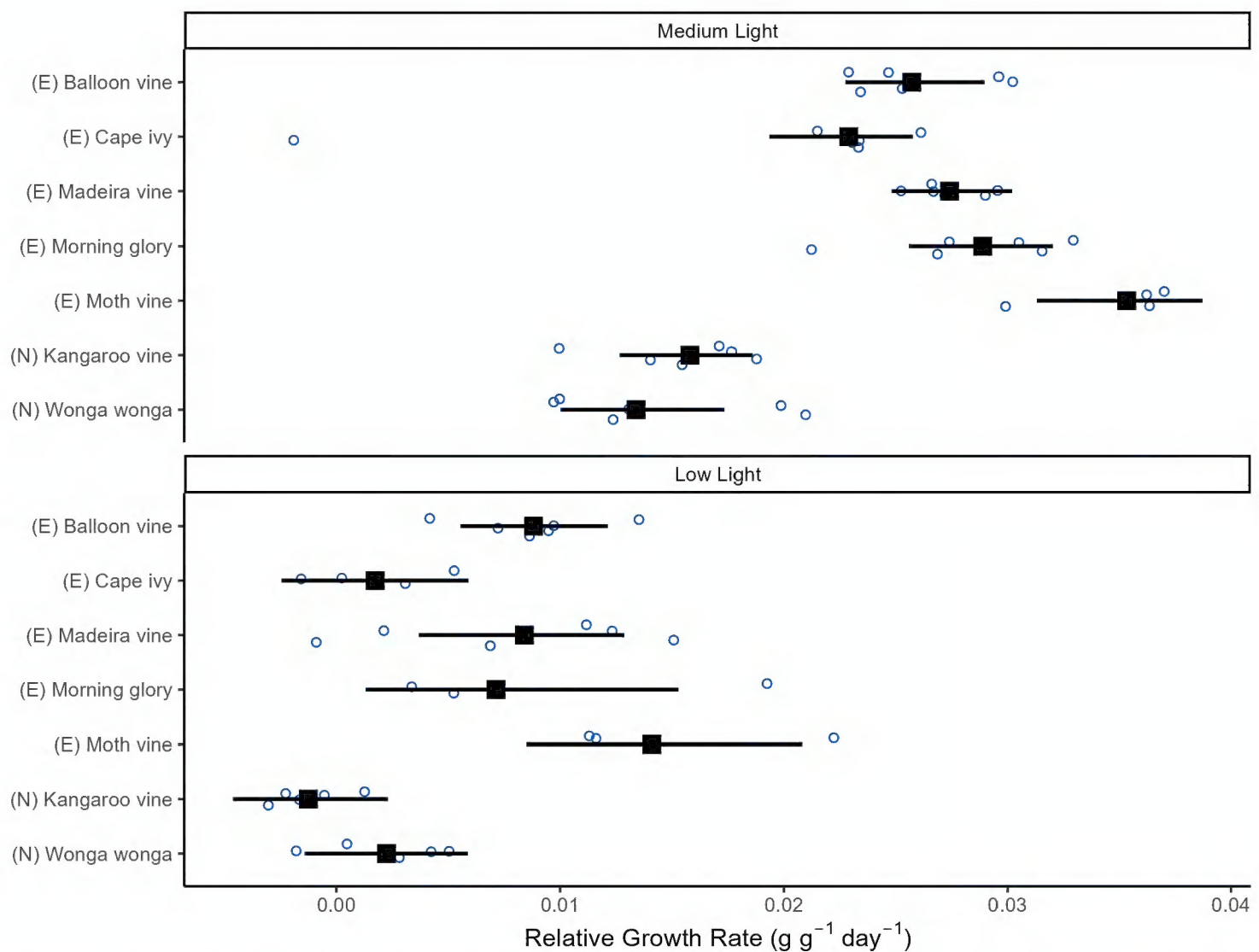

Figure 1. Mean relative growth rate (RGR) with 95% bounds on the mean predicted values from each model (black lines) and observed RGR value for individual plants (blue dots) for both light treatments. (E) are exotic vines, (N) are native vines.

Table 1. The predicted mean trait values and the 95% bounds on the mean predicted values from each model (smaller font). RGR = relative growth rate (g g⁻¹ day⁻¹), stem growth = increase in stem length per day (cm/day), LMF = leaf mass fraction (%), RMF = root mass fraction (%), SMF = stem mass fraction (%), SLA = specific leaf area (cm²/g), (E) denotes exotic species, (N) denotes native species. * note that RMF for Anredera cordifolia includes the weight of aerial tubers.

Species	Light treatment	Predicted mean trait values					
		RGR	Stem growth	LMF	RMF	SMF	SLA
Anredera cordifolia (E)	Medium	0.0274	1.55	16.5%	65.8%	17.7%	323.0
		0.0248–0.0302	1.29–2.31	14.9–22.5	44.3–56	26.3–36.2	272.7–379.4
	Low	0.0084	0.47	32.9%	42.5%	24.7%	988.1
		0.0037–0.0129	0.42–0.97	22.9–39.5	32.8–51.2	19.8–35.7	814.2–1205.3
Araujia sericifera (E)	Medium	0.0353	1.14	18.8%	37.0%	44.3%	255.0
		0.0313–0.0387	0.82–2.05	13.3–23.7	30.8–44.1	37.6–51.4	209.83–302.27
	Low	0.0141	0.24	11.3%	52.7%	36.0%	625.8
		0.0085–0.0208	0.14–0.81	6.4–21.1	36.6–67.4	20.8–50.1	463.8–824.1
Cardiospermum grandiflorum (E)	Medium	0.0257	1.62	24.4%	24.1%	51.5%	329.5
		0.0227–0.0290	1.25–2.71	19.7–29.3	19.4–29.1	45.7–57.2	281.2–383.9
	Low	0.0088	0.48	42.2%	12.6%	45.2%	745.7
		0.0056–0.0121	0.36–1.24	31.3–52.3	7.3–20.5	34.2–55.7	643.9–864.0
Delairea odorata (E)	Medium	0.0229	1.92	15.3%	12.5%	72.3%	570.4
		0.0193–0.0258	1.46–3.20	11.6–19.4	9.2–16.6	66.7–76.9	480.4–663.3
	Low	0.0017	0.62	25.6%	12.1%	62.3%	1607.5
		-0.0024–0.0059	0.43–1.75	15.6–36.7	5.9–21.3	48.7–73.8	1279.6–2013.8
Ipomoea cairica (E)	Medium	0.0289	2.62	11.9%	45.7%	42.5%	379.3
		0.0256–0.0320	2.02–4.25	9.1–16.1	39.6–51.0	36.5–48.0	321.5–443.6
	Low	0.0071	0.74	29.6%	33.5%	36.9%	1219.6
		0.0013–0.0153	0.48–2.24	16.4–41.8	21.4–49.7	22.7–51.3	957.4–1540.2
Cissus antarctica (N)	Medium	0.0158	0.80	45.6%	13.4%	41.0%	189.8
		0.0127–0.0186	0.61–1.32	38.5–50.3	10.5–18.2	36.0–47.1	161.6–219.9
	Low	-0.0013	0.11	45.2%	25.3%	29.6%	362.7
		-0.0046–-0.0023	0.07–0.36	34.8–57.8	15.0–35.5	19.0–40.0	285.2–462.7
Pandorea pandorana (N)	Medium	0.0134	0.91	30.8%	24.6%	44.6%	281.7
		0.0100–0.0174	0.69–1.54	25.2–35.6	20.2–30.0	38.9–50.5	242.1–327.8
	Low	0.0022	0.20	42.3%	28.5%	29.2%	482.6
		-0.0014–0.0059	0.14–0.58	31.1–53.9	18.5–39.6	19.0–39.9	389.1–585.4

cies, *P. pandorana* (84% reduction) and *C. antarctica* (~ 98% reduction) showed large reductions in RGR under low light. *C. antarctica* barely grew in the low light treatment making estimates of percentage reductions difficult to calculate. The three other exotic species had reductions of between 60 and 69%. Higher variability in RGR was seen amongst individuals of exotic invasive species in the low light (see Suppl. material 1).

All the exotic invasive species grown in the medium light treatment had higher predicted mean RGR values than the two native species (Fig. 1, Table 1). *A. sericifera* had the highest predicted mean RGR with only *I. cairica* having a slight overlap in the 95% range of predicted mean values. All other exotic invasive vine species had relatively similar predicted mean RGR values with a high percentage of overlap in the 95% bounds on the predicted mean. In the low light treatment, *A. sericifera* still tended to have the highest RGR, though the 95% bounds on the predicted mean substantially overlapped with three of the other exotic invasive species (Fig. 1, Table 1, Suppl. material 2).

Length of main stem

Similar to RGR, the predicted median stem length grown per day for all species in the medium light treatment was greater than the low light treatment, with no overlap in the 95% bounds on the predicted median values from the model (Fig. 2). In the medium light treatment, *I. cairica* had the highest predicted median stem growth per day at 3.2 cm/day and had final raw stem lengths across individuals of 3.6–8.5 m. *D. odorata* also had high stem growth rates, with a slight overlap on the 95% bounds on the predicted median with *I. cairica* and final stem lengths of 3.9–6.4 m. *A. sericifera* had the lowest predicted median stem growths for the exotic invasive species. The two native species clearly had the lowest predicted median stem growth (Fig. 2), with there being a slight overlap in the 95% bounds on the predicted median with *A. sericifera* only (Suppl. material 1).

In the low light treatment, *I. cairica* and *D. odorata* had the highest predicted median stem growth per day with high variability amongst individuals. Other species had closer predicted median values. The gap between exotic invasive and native species in the low light treatment was actually higher than the medium light treatment (Fig. 2), though *A. sericifera* only had slightly higher predicted stem growth than *P. pandorana* at 4 mm per day (Fig. 2). Mean predicted values were very similar to median values (Fig. 2, Table 1).
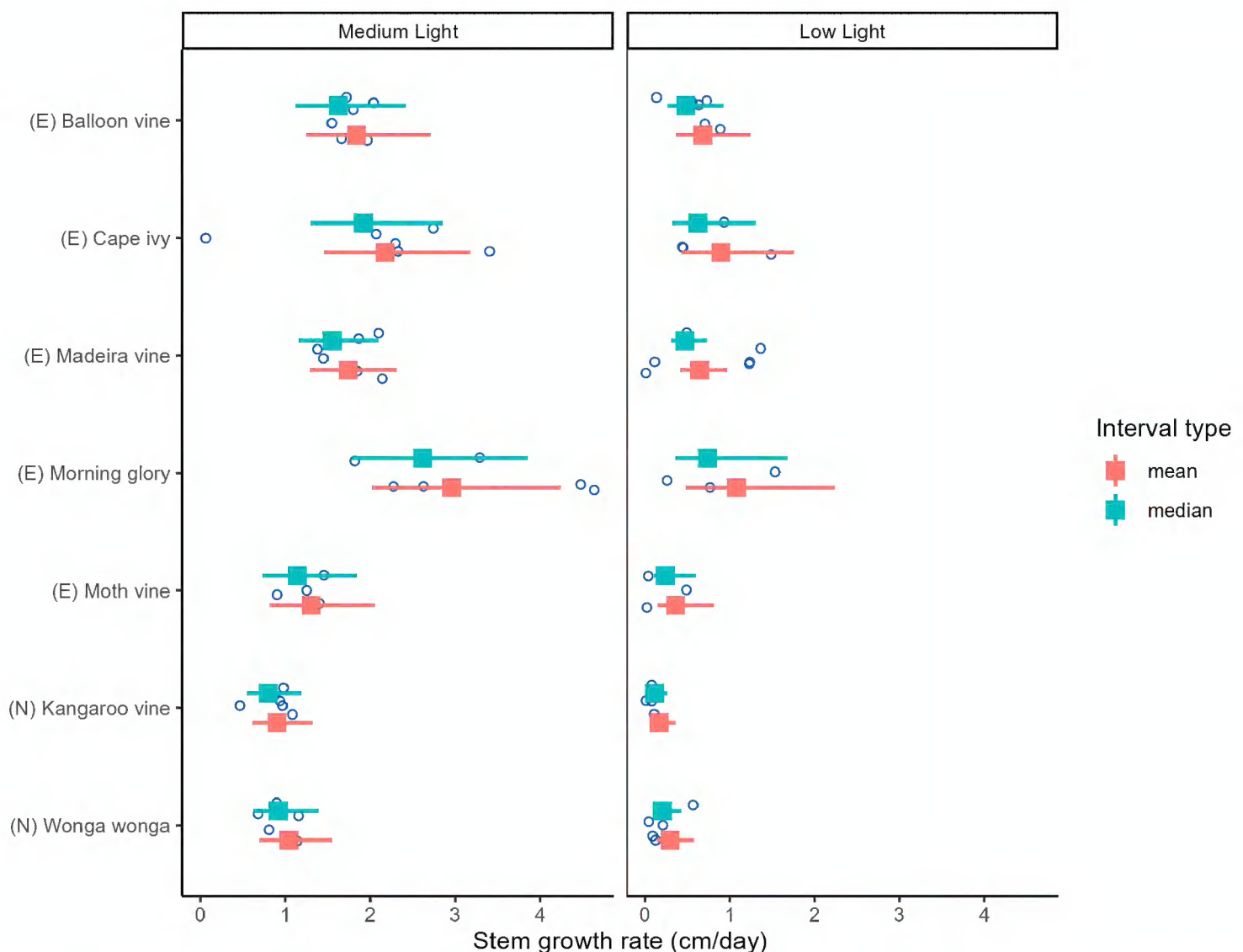

Figure 2. Median (blue lines) and mean (red line) stem growth rate with 95% bounds on the mean predicted values from each model, for both light treatments. Blue dots show the observed value for individual plants. (E) are exotic vines, (N) are native vines.

Biomass allocation

The percentage of biomass invested into leaves, stems and roots differed amongst species and light treatments (Fig. 3, Table 1). In the medium light treatment, exotic invasive species invested very little into leaves, with all species having a predicted mean proportion of leaf biomass less than 25%, while the two natives, *C. antarctica* and *P. pandorana* had predicted mean leaf biomass proportions of 47% and 31%, respectively. *Anredera cordifolia* and *I. cairica* invested relatively highly into root biomass with the predicted mean being 66% and 46%, respectively. For *A. cordifolia* in the medium light, the mean number of aerial tubers produced was 45.3 (range 29–61). Aerial tubers accounted for between 5 and 30% of the total biomass (mean = 15%). The roots, excluding aerial tubers, accounted for, on average, 55% of total biomass. No aerial tubers were produced by individuals grown in the low light treatment. Two species, *D. odorata* and *C. antarctica* invested very little into roots (Fig. 3). *Delairea odorata* invested the greatest amount into stems (predicted mean of 72%) (see Suppl. material 1).

Biomass allocation for all species in the low light treatment was more varied, seen by wider 95% bounds on the predicted mean values (Fig. 3). Natives did invest more biomass in leaves compared to moderate light treatments, but overall, the allocation to
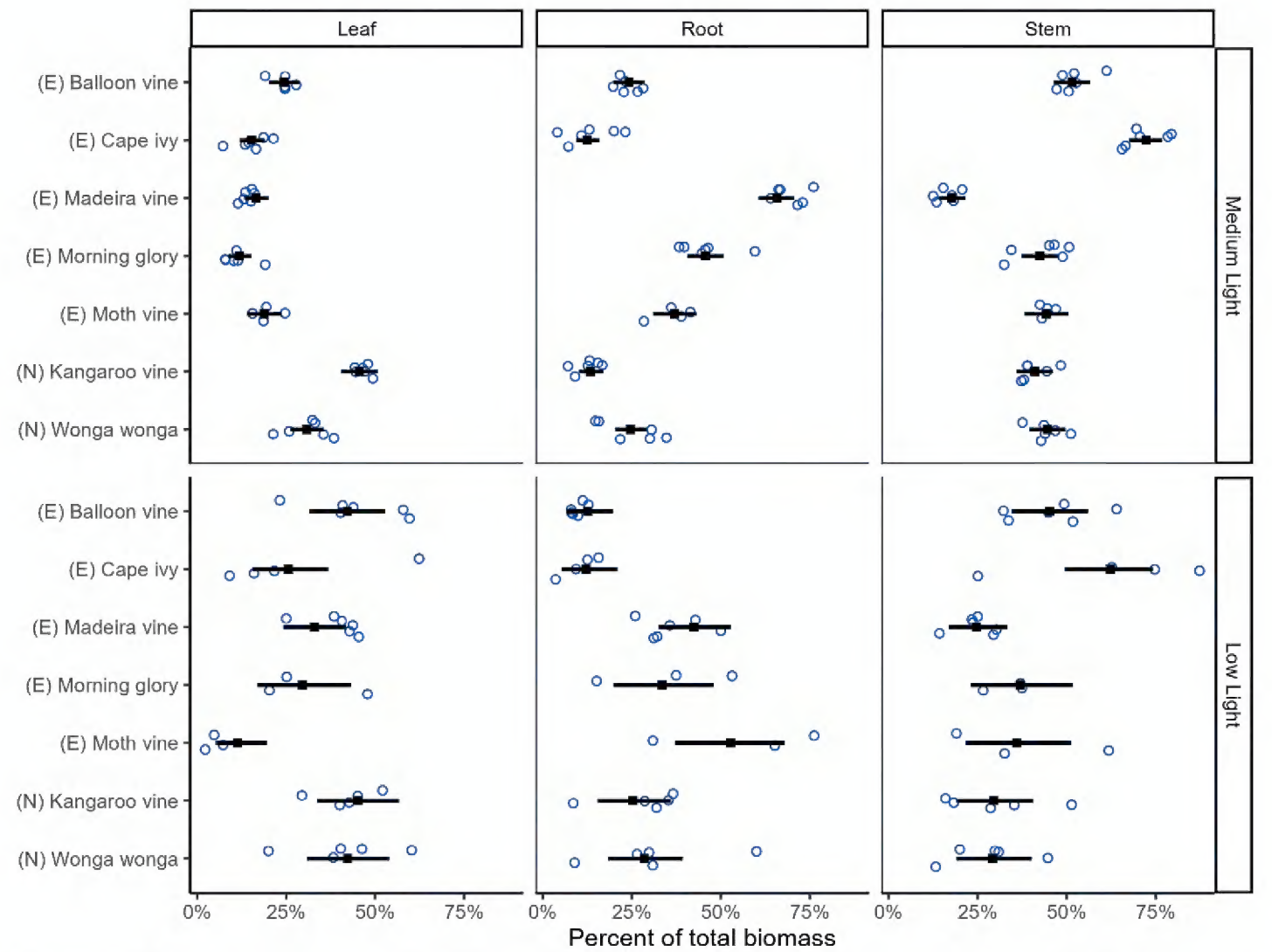

Figure 3. Mean proportion with 95% bounds (black lines) on the mean predicted values from each model, of biomass invested into leaves, roots and stems for all species in both light treatments. Blue dots are observed proportions for individual plants.

leaves across all vines was similar. *A. sericifera* tended to allocate resources into stems and roots rather than leaves. *Delairea odorata* and *C. grandiflorum* invested very little in roots, focusing on stem growth by comparison (Fig. 3, Table 1, Suppl. material 2).

Specific leaf area

The 95% bounds on the mean predicted range for SLA was substantially higher in the low light treatment than the medium light for all species (Fig. 4, Table 1), with there being no overlap in the 95% bounds on predicted means between treatments for each species (Suppl. material 2). The greatest difference in predicted mean SLA between the treatments was seen in *I. cairica* (222% difference) and *A. cordifolia* (206%). *D. odorata* (182%), *A. sericifera* (145%) and *C. grandiflorum* (126%) had a moderate predicted increase in SLA, while the two natives had the lowest difference in SLA amongst treatments; *C. antarctica* (91%), then *P. pandorana* (71%).

In general, exotic invasive species had higher SLA than native species, except for *A. sericifera* in the medium light which had a considerable overlap in the 95% bounds on predicted mean values with *P. pandorana*, though only a slight overlap in the low
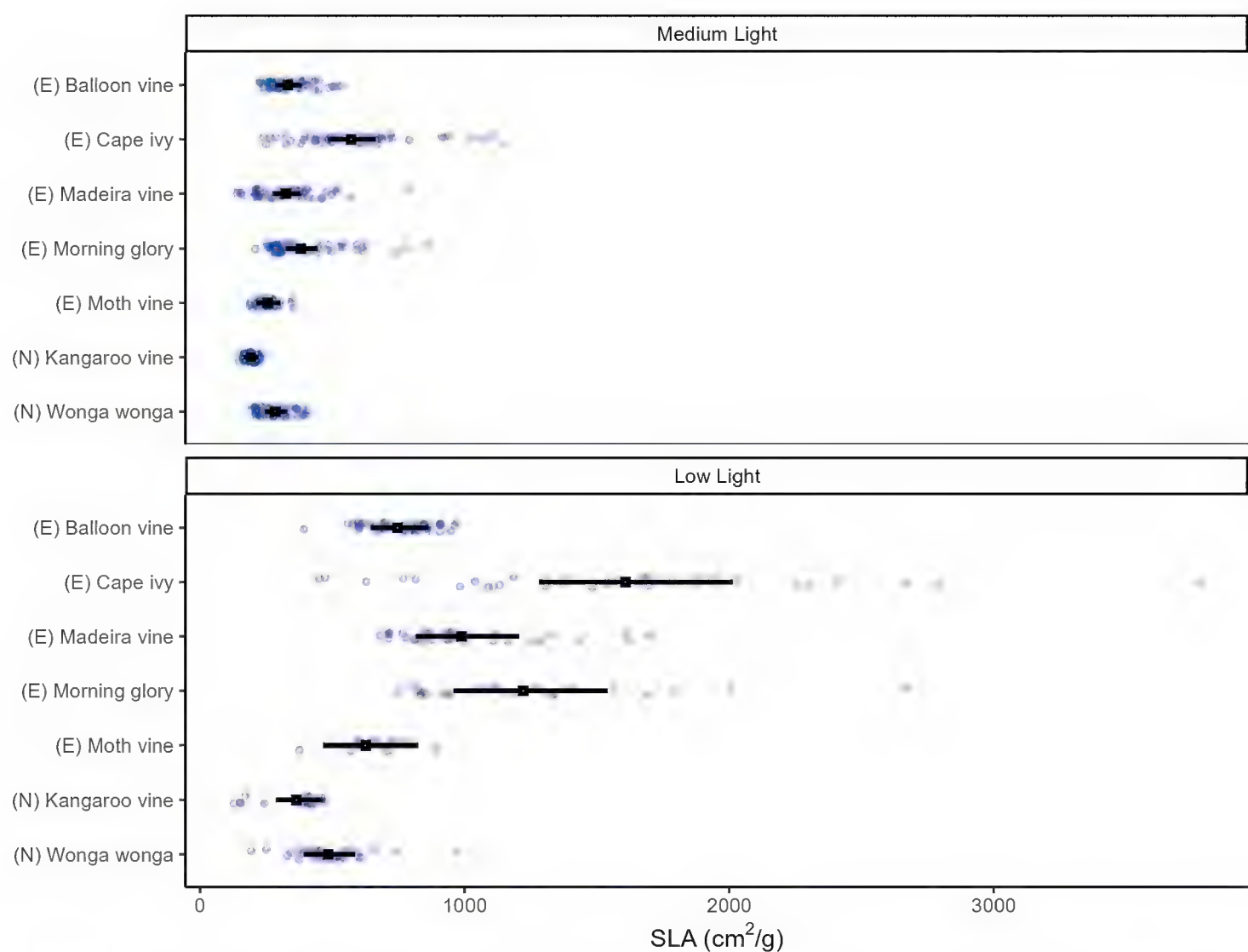

Figure 4. Observed specific leaf area (SLA) with 95% bounds (black line) on the mean predicted values from each model for all species in both light treatments. Blue dots are observed values for individual plants. (E) are exotic vines, (N) are native vines.

light treatment. *Delairea odorata* and *I. cairica* had the two highest predicted mean SLA in both treatments (Fig. 4, Table 1). *Cardiospermum grandiflorum* and *A. cordifolia* had similar SLA in the medium light, though *A. cordifolia* had much higher SLA in the low light (Fig. 4, Table 1).

Discussion

All species grew at faster rates under the higher light conditions that are reflective of rainforest edges, suggesting that quick invasion was most likely from disturbed edges or light gaps for all species. Low light conditions slowed growth, but the reduction in growth varied amongst species reflecting a differential risk of invasion and establishment into the rainforest interior. The two common native species had very low growth rates in all light levels, but particularly in the low light. They also showed a limited capacity to vary SLA and improve light capture relative to the invasive species. This suggests they would most likely establish in edges and better lit areas. This is despite one of these species being considered problematic; *Cissus antartica* can significantly smother vegetation along rainforest edges. Our results suggest that this issue will not occur under the canopy.

All exotic invasive species had higher relative growth rates than native species. Relative growth rate and high SLA are correlated with invasiveness (Poorter and Bongers 2006; Leishman et al. 2007; Van Kleunen et al. 2010; Dawson et al. 2011). However, some of the same species were used in Osunkoya et al. (2010) which measured no difference in RGR amongst native and exotic species in the tropics. Our work suggests that, at least in temperate areas, high relative growth rates were a characteristic of our invasive species.

Compared to self-supporting woody plants, the native vines in this study still sit on the "faster" side of the life history spectrum. For example, in a comparison of co-existing tropical trees and vines, Mello et al. (2020) found that the mean SLA for trees was 141 cm²/g (± 62.41 SD) and vines was 177 cm²/g (± 80.77 SD). In our study, the mean SLA for *C. antarctica* (190 cm²/g) and *P. pandorana* (282 cm²/g) grown in medium light was higher than that of the vines measured by Mello et al. (2020). Nevertheless, the difference in SLA between the exotic invasive and native species in this study may be due to natives investing more into leaf defence from herbivores leading to lower SLA, leaving the exotic invasives at an advantage with fewer herbivores in their introduced range (Keane and Crawley 2002).

Coupled with the higher growth rates measured, all exotic invasive vine species showed flexibility in leaf SLA when grown in low light conditions. All had higher SLA values under low light and were higher than both native species in all light conditions. Interestingly, the means in low light were associated with a great deal of variability amongst individuals (large 95% confidence intervals). Invasive exotic species, therefore, show plasticity in their responses to low light conditions, increasing the size of their leaves relative to the leaf biomass to increase light capture capacity. As a result, in comparison to the native species, all exotic invasive species will be capable of better

light harvesting under rainforest canopies, increasing photosynthesis and growth rates. Furthermore, increased SLA, even under medium light conditions, may also help them in forest gaps as they grow leaves better suited to the light environment they are in and, therefore, may be able to respond to canopy disturbances better (Liu et al. 2016b). Phenotypic plasticity of leaves is a trait often observed in invasives (Daehler 2003; Richards et al. 2006; Davidson et al. 2011) and Osunkoya et al. (2014) also found that leaf plasticity of exotic invasive vine species (including *A. cordifolia* and *A. sericifera*) was higher than phylogenetically similar native vine species. Therefore, while more native and exotic vine species need to be compared, it is likely that higher plasticity in leaves correlates with invasiveness and explains why exotic invasive vines often dominate in disturbed forests with patchy canopy cover, but may also increase their capability to invade low light less-disturbed closed forests.

We identified three growth strategies amongst the exotic invasive vines that we investigated, with regards to their risk to rainforest communities. These strategies may be a more general approach for other species, but further species would need to be considered to establish such strategies. Thus our descriptions of a strategy highlight some of the differences in growth responses of the exotic species we tested which may increase risk of invasion. The first strategy was associated with fast growth, exemplified by *D. odorata* and *I. cairica* which showed high SLAs and high mean stem growth rates under both canopy and edge conditions. Having fast stem growth rates and high stem biomass allocation is beneficial for vines as it allows individuals to compete with others through early access to canopy light (Falster and Westoby 2003; Llorens and Leishman 2008). High SLA provides leaves with more efficient energy capture to invest into growth (Poorter and Bongers 2006), although it also indicates that these species are likely to be short-lived (Westoby et al. 2004). *D. odorata* also invested very little into roots and did not produce woody stems suggesting a quick strategy with low competitive capacity. However, both of these species grow horizontal running stems which can form roots and support new stems, perhaps advantageous in capturing more area quickly under higher light conditions. This allows them to spread quickly and persist despite leaves (and perhaps stems) being replaced regularly. These species will be quick to establish both under canopy and at edges, but are likely to be more successful in forest gaps and edges and may do poorly through time under the canopy.

A second, more long-term invasion strategy was evident in the three other exotic species. These three had the highest relative growth rates under low light conditions, providing opportunities for invasion even within undisturbed rainforest patches; *Anredera cordifolia, Araujia sericifera* and *Cardiospermum grandiflorum*. While some *A. sericifera* individuals may be particularly effective at growing under the canopy, we also recorded some mortality in low light conditions. Surviving individuals produced few leaves, focusing resources on roots and stems suggesting a response to reach the canopy as quickly as possible. High dispersal capability using large numbers of wind-blown seeds (Vivian-Smith and Panetta 2005), coupled with high RGR in higher light, explains why *A. sericifera* is listed as a major weed in multiple countries (Vivian-Smith and Panetta 2005), where it damages vegetation and restricts regeneration, as well

being poisonous to humans and livestock (NSW DPI 2020). Germination has been shown to be significantly reduced in cool (< 20 °C) and dark conditions (Vivian-Smith and Panetta 2005), suggesting that the maintenance of canopy cover can decrease establishment. Our results suggest that if it can establish under canopy, then it may well persist increasing its risk in rainforest interiors. If given the right conditions, *A. sericifera* is likely the species to build biomass fastest out of the species grown in this study and presents one of the highest invasion risks under rainforest canopies.

One other invasive species in this group of potential understorey invaders was *Anredera cordifolia*. This species was also able to have quite high RGRs under low light increasing its allocation to leaves and stems in this environment, compared to the location at the edges of rainforests. It also had much greater flexibility in changing leaf light capture under the canopy, compared to *A. sericifera*. At edges in ideal conditions, it can maximise growth rates through having amphistomatous leaves and high numbers of stomata (Boyne et al. 2013), increasing photosynthetic ability and efficiency. *A. cordifolia*, however, utilises an additional strategy. Under better growing conditions, resources are used to develop canopy-held tubers which are a robust dispersal strategy, providing new vegetative recruits which receive greater resources maternally than germinants. The strategy enables the species to persist through inclement conditions (Vivian-Smith et al. 2007). In the six months of this experiment, individuals in the medium light produced an average of 45 aerial tubers, highlighting the high propagule pressure of this species, as well as the speed in which it can reach reproductive maturity, which is a trait often used to explain invasiveness and feasibility of control (Panetta and Grigg 2021). Therefore, *A. cordifolia* can persist under canopies through reallocation of resources to leaves and stems and can spread throughout a site, particularly from the edges, making it difficult to eradicate and contain (Panetta and Grigg 2021). Tubers (included within the root component) resulted in lower allocation to stem growth, but provided a capacity to persist at the edges and create new individuals increasing invasion and risk. This places this species as one of the highest risk species under rainforest canopies.

Conclusion

Our work measured important growth parameters for a range of exotic vines and we were able to identify different strategies that influence how invasive exotic vine species may invade rainforests. While all species perform better in higher light conditions reflective of rainforest edges and gaps, the capacity to maintain higher levels of growth under rainforest canopies showed that some species may well establish and persist causing host tree damage within the rainforest. Coupled with vegetative growth strategies, we identified differences in the capacity of species to establish and persist under canopies. We suggest that maintaining canopy health and controlling edges, still remains the key tool for reducing vine invasion, although at least two species, *Araujia sericifera* and *Anredera cordifolia* have characteristics that suggest that directed control within rainforests is needed.

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Supplementary material 1

Difference in mean and 95% bounds, as well as the percentage overlap of mean values reported as a probabilty (Probability higher) between species for the physiological measurements taken

Authors: Adam Bernich, Kris French, Michael Bedward

Data type: xlsx

Explanation note: Species are compared within light treatments only. Probabilty higher reflects the values of the Species 1 being higher than Species 2. Asterisks in Species 1 column denotes exotic species.

Link: https://doi.org/10.3897/neobiota.90.110659.suppl1

Supplementary material 2

Difference in mean and 95% bounds, as well as the percentage overlap of mean values reported as a probabilty (Probability higher than LL) for the seven species grown in the study

Authors: Adam Bernich, Kris French, Michael Bedward

Data type: xlsx

Explanation note: Asterisks denote exotic species.

Link: https://doi.org/10.3897/neobiota.90.110659.suppl2

Supplementary material 3

The dry weight of the individuals used as the initial values to calculate relative growth rates for each species

Authors: Adam Bernich, Kris French, Michael Bedward

Data type: xlsx

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